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Rapid response to shoot removal by the invasive wetland plant, alligator weed (*Alternanthera philoxeroides*)

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Abstract

Resprouting plants provide an interesting test to the generality of plant allometric relationships. The ability to rapidly resprout after disturbance also makes weeds more difficult to control. We performed a glasshouse experiment to investigate regrowth of an invasive plant (alligator weed, *Alternanthera philoxeroides* (Martius) Grisebach) after an experimental mowing treatment. Nutrient levels and biomass accumulation were measured weekly for five weeks, and carbohydrate levels were measured when regrowth was quickest. After five weeks, the biomass of treatment plants was similar to that expected from a growth curve fitted to undamaged control plants. Treatment plants, however, had a higher below-ground biomass, and a higher ratio of stem to leaf biomass than expected. The regrowing material also had a lower nutrient concentration. Both the rapid regrowth and the change in morphology make the mechanical control of alligator weed more difficult, and may, in part, be responsible for the invasiveness of this plant.

Keywords: Resprouting; Root:shoot ratio; Top-kill

1. Introduction

An ability to persist in a regularly disturbed environment can prove an advantage over species recruiting from seed (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Vesk and Westoby, 2004b). Species with clonal growth are particularly suited to habitats with abundant resources and chronic low intensity disturbances, such as grazed wetland areas (Philbrick and Les, 1996). For a plant to be able to regrow quickly, it has to retain the potential to regrow and have reserves that can be used for regrowth. There is only a small direct cost to maintaining meristematic buds (Vesk and Westoby, 2004a), but maintaining carbohydrate reserves may be expensive (Canadell and Lopez-Soria, 1998; Iwasa and Kubo, 1997). However, in locations where resprouting provides an ecological advantage, resprouting may also increase the potential of a plant to be invasive (Rejmánek et al., 2005; Sakai et al., 2001).

There is a robust direct correlation between leaf, stem, and root annual growth rates across a wide range of species (Niklas and Enquist, 2002). Within this range, theoretical models predict that plants allocate resources between plant parts to increase fitness according to resource availability (the model of functional equilibrium) (Agren and Franklin, 2003; Aikio and Markkola, 2002; Iwasa and Kubo, 1997; Poorter and Nagel, 2000). These studies suggest that, after damage, species should invest resources in stem and leaf material to return the root to shoot ratio to an optimal level, i.e. one that maximises total plant growth. Indeed, Poorter and Nagel (2000) showed that this is how barley plants regrow after damage. Two questions that have been less well studied, but are of particular interest to weed managers, are how quickly do plants return to an optimal root:shoot, and what is the energetic cost of recovery to the plant?

Here we examine the response of an invasive plant, alligator weed (*Alternanthera philoxeroides* (Martius) Grisebach (Amaranthaceae)), to canopy removal (mowing). We explored three main measures for the partitioning of plant resources: biomass, nutrients, and carbohydrates.

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Alligator weed is an amphibious stoloniferous plant from South America that is primarily associated with aquatic habitats, but can spread into moist terrestrial environments (Julien et al., 1995). It invades agricultural areas and blocks drainage and irrigation channels causing problems on agricultural land (Spencer and Coulson, 1976). In most of its introduced range it reproduces asexually, primarily from stem nodes and shoot fragments (Julien et al., 1992).

The aquatic form of alligator weed is well controlled in warm temperate climates by an introduced biological control agent, the alligator weed flea beetle *Agasicles hygrophila* (Coleoptera: Chrysomelidae) (Julien et al., 1995), but this beetle rarely attacks the terrestrial form (Julien and Bourne, 1988). If the terrestrial form is to be controlled mechanically, it is important to know how quickly plants regrow. The speed and nature of the regeneration may also allow alligator weed to out-compete native plants.

2. Materials and methods

This study was conducted in the glasshouses of CSIRO Long Pocket Laboratories, Brisbane, Qld, Australia, between October 2003 and January 2004. The experiment took place during the summer months because this is the primary growing season for alligator weed in Australia (Julien et al., 1992).

Plants were propagated from stems collected at Raymond Terrace, New South Wales, Australia (−32.828°S and 151.841°E), on 22 October 2003. Stems were cut into 4 cm lengths containing one node each, and placed in fungicide (30 mg L^{-1} benomyl, as Benlate, DuPont) for a minimum of 1 h. Cuttings were then dipped in rooting solution (2 g L^{-1} indole butyric acid, as Rootex-L, Bass Laboratories) for 15 s and planted horizontally in potting tubes of 10 cm diameter at a depth of 1 cm (50:50 sand:peat mixture, 10 g L^{-1} dolomite).

Plants were grown for 22 days before being re-potted in 15 cm diameter pots (same soil mixture). Over 90% of the cuttings had germinated, with the majority showing significant growth. The smallest 5–10% plants were discarded. From the plants to be used in the experiment, 40 were selected at random and harvested. Plants were grown for a further 25 days before the treatment was applied on 8 December.

The shoots of treatment plants were removed by cutting the canopy just above soil level, similar to mowing. Plants were then randomly assigned locations on benches and spaced so each plant was approximately 15 cm from its neighbours. Forty control plants were harvested on the same day as the treatment (referred to as baseline plants). Twenty control plants and 20 treatment plants were harvested at the end of each week for the following five weeks. Plant material was separated into leaves, stems (all other above-ground parts), and roots (all below-ground parts), dried to constant weight at 60 °C, and weighed to the nearest 0.01 g. The nitrogen, phosphorus, and potassium content of stem, leaf, and root material was measured for 48 of the plants (12 baseline plants and 6 plants per treatment from weeks 1, 3, and 5). The nutrient analysis was conducted by the Queensland Department of Natural Resources, Analytical Services, Brisbane, Australia.

The above-ground (leaf and stem) and the roots of 24 plants were analysed for cold water soluble carbohydrate (WSC) and total carbohydrates (New South Wales Department of Agriculture Analytical Chemistry Laboratory, Wagga Wagga, Australia): 8 from baseline plants, and 8 each from control and treatment plants sampled after 20 days. These plants were not used in the rest of the analysis as plant material was submerged in boiling ethanol for 2 min shortly after harvesting to inhibit enzyme activity (Allen, 1989). Data were analysed using concentrations of WSC and non-water soluble carbohydrates (non-WSC). Non-WSC concentrations were calculated as total carbohydrates minus total WSC.

The computer program R was used for all analyses (v. 2.0.1, The R Development Core Team, 2004). Four potential relationships between the growth of biomass in control plants and time were tested: a linear, a log-linear, a linear with the square root of biomass, and a logistic. To see how well the models describe the growth of smaller plants, extrapolations were made to describe plants sampled during re-potting. The growth model that best describes control plant data was used to predict how plants with their shoots removed should grow.

Baseline plants were used to estimate the percentage reduction in biomass, nutrient content, and carbohydrate content caused by shoot removal. Differences in nutrient concentration between control and treatment plants were tested by fitting linear models to the relationship between logit-transformed nutrient concentrations and biomass separately for each plant part. This was done as nutrient status is affected by plant size, different plant parts have different nutrient concentrations, and shoot removal affects the distribution of biomass between plant parts (Lambers et al., 2000).

3. Results

A linear relationship between time and square root of biomass provided a good description of the growth of control plants ($r^2 = 0.94$):

$$W_t = (W_0^{0.5} + x \cdot t)^2 \quad (1)$$

where W_0 is the plant biomass at time 0; t the time since the start of the experiment; and x is a constant [0.671 ± 0.014 $g^{0.5}$ day^{-1} (1S.D.); Fig. 1]. A logistic model also provided a good fit to the experimental data ($r^2 = 0.94$), but Eq. (1) was much better at predicting the size of plants sampled before the start of the experiment [observed plant dry weight were 0.23–1.7 g; Eq. (1) predicted 1.2–1.4 g; and the logisitic model predicted 3.8–4.9 g (95% C.I.s)]. Linear and log-linear models of biomass against time did not have randomly distributed residuals.

Shoot removal reduced total plant biomass by around 65%. There was a large reduction in plant nitrogen, phosphorus, and potassium content (about 80%), but a smaller reduction in carbohydrate levels (Table 1).

One week after treatments were applied, treatment plants had lower root biomass than baseline plants (3.61 g versus 4.77 g, $t_{53} = 0.48$, $p < 0.01$), but treatment plants had a similar total weight to the below-ground part of baseline plants (4.60 g versus

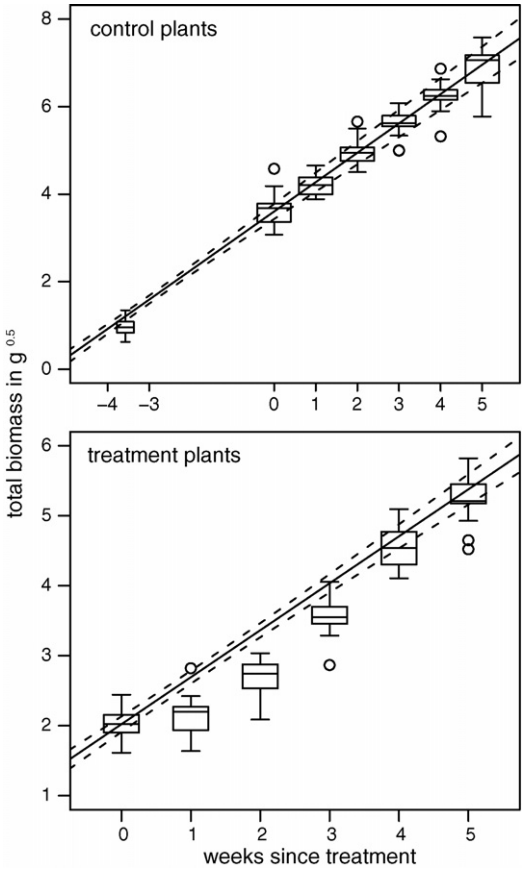

Fig. 1. The change in plant biomass with time. Solid lines are from Eq. (1), and dotted lines are 95% C.I.s. Plants sampled 25 days before the start of the experiment are on the far left of the control plot, but these data were not used to fit Eq. (1). The biomass of treatment plants at week 0 is the weight of the below-ground part of baseline plants. This weight is used as the starting weight (W_0) to predict the growth of treatment plants from Eq. (1). Note the differences in scales of the *y*-axes: after five weeks, treatment plants are 8–38 g smaller than control plants, but treatment plants are of similar size to that predicted if the growth curve is adjusted to take biomass removal into account.

4.77 g, $t_{53} = 0.48$, $p = 0.63$). After this initial reduction in growth, treatment plants grew slightly faster than expected by Eq. (1). After one month, treatment plants were of a similar size to that expected from the growth model if W_0 was set to 4.77 g, the root biomass of baseline plants (Fig. 1).

Table 1
The effect of shoot removal on plant variables

Variable	Mean	Range	±1S.D.	*n*
Biomass	65 (a, d)	53–74	60–69	36
Carbon	63 (a, d)	54–73	57–68	12
Nitrogen	81 (b)	71–86	77–84	12
Phosphorus	86 (b)	70–88	79–88	12
Potassium	81 (b)	74–87	76–85	12
Carbohydrates	49 (c)	39–65	40–58	8
Water soluble carbohydrates	50 (c)	39–65	41–59	8
Non-water soluble carbohydrates	40 (c, d)	8–73	16–70	8

Values shown are the percentage of a variable removed by shoot removal. Different letters indicate significant differences between the groups (paired sample *t*-tests, $p < 0.05$).

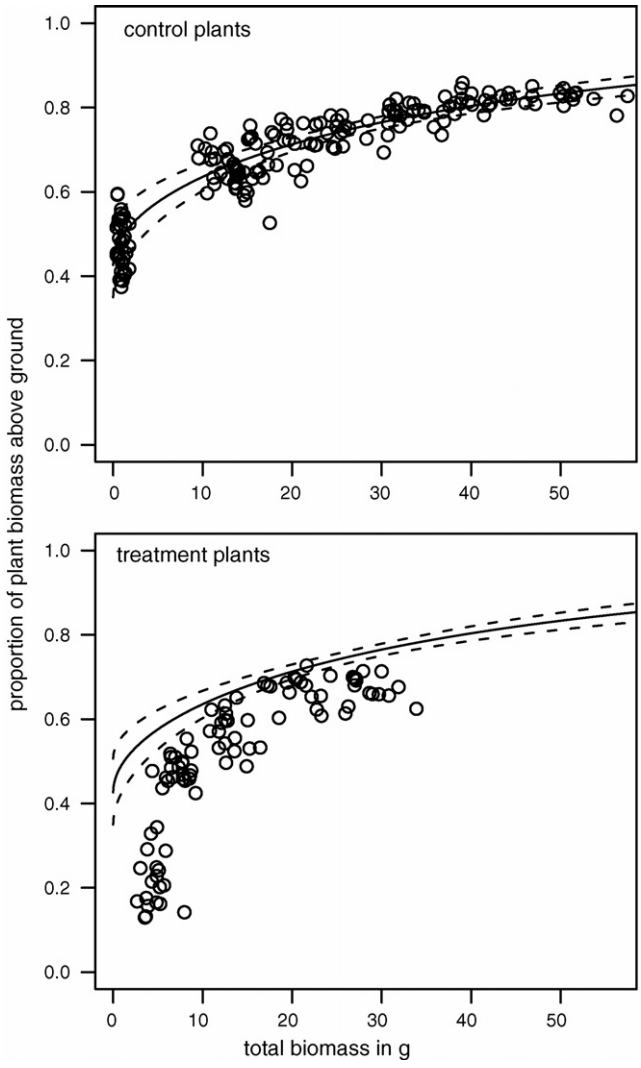

Fig. 2. The effect of plant size on the proportion of biomass above the ground. Solid lines are from a model fitted to the square root of the data on control plant biomass and dotted lines are 95% C.I.s. Plants sampled 25 days before the start of the experiment are on the far left of the control plot, but these data were not used to fit the model. For the control plot, $r^2 = 0.74$.

There is a very strong relationship between plant size and phenology: larger plants had more above-ground biomass than below-ground biomass, and larger plants had more stem than leaf biomass (Figs. 2 and 3). While treatment plants would be expected to initially have a higher proportion of root than control plants, this effect had not disappeared by week 5 (Fig. 2). At the end of the experiment, treatment plants also had more stem material than expected (Fig. 3).

In control and treatment plants, concentrations of nitrogen, potassium, and phosphorus in leaves were higher than in stems, and concentrations in stems were higher than in roots (nitrogen levels are shown in Fig. 4, other nutrients are not presented). Nutrient concentrations also declined as weight increased. Treatment plants had a lower nitrogen concentration than control plants (Fig. 4; roots, $F_{(2,46)} = 10.66$, $p < 0.01$; stems, $F_{(2,46)} = 58.9$, $p < 0.01$; and leaves, $F_{(2,46)} = 16.6$, $p < 0.01$). Phosphorus and potassium concentrations showed a

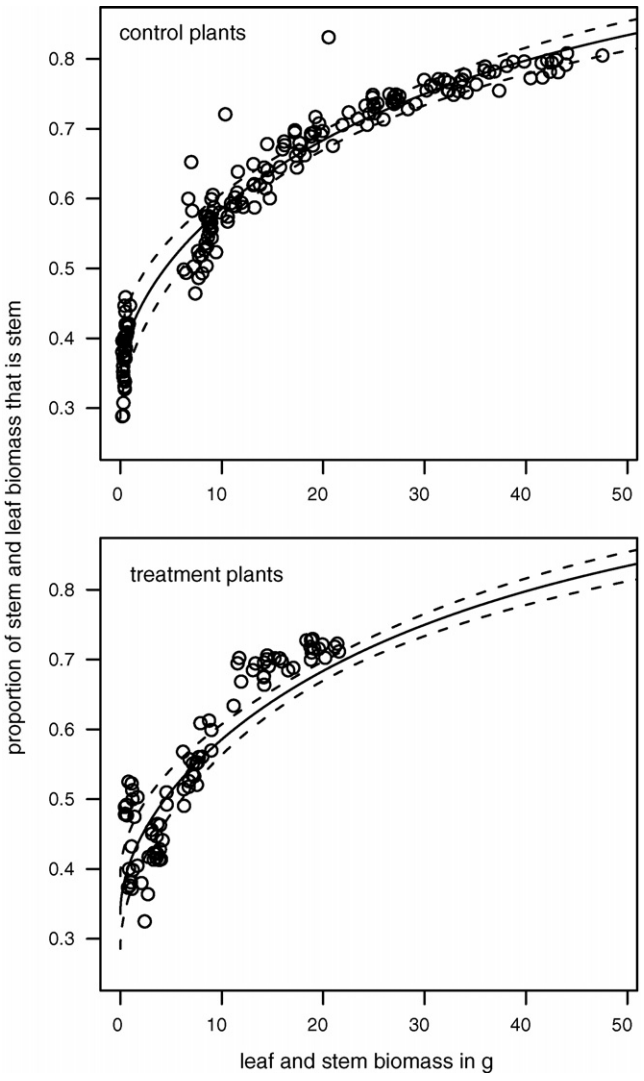

Fig. 3. The effect of plant size on the proportion of above-ground biomass that is stem material. The solid lines are from a model fitted to the control data, and the dotted lines are 95% C.I.s around the model. Plants sampled 25 days before the start of the experiment are shown on the far left of the control plant plot, but were not used to fit the model. For the control plot, $r^2 = 0.89$.

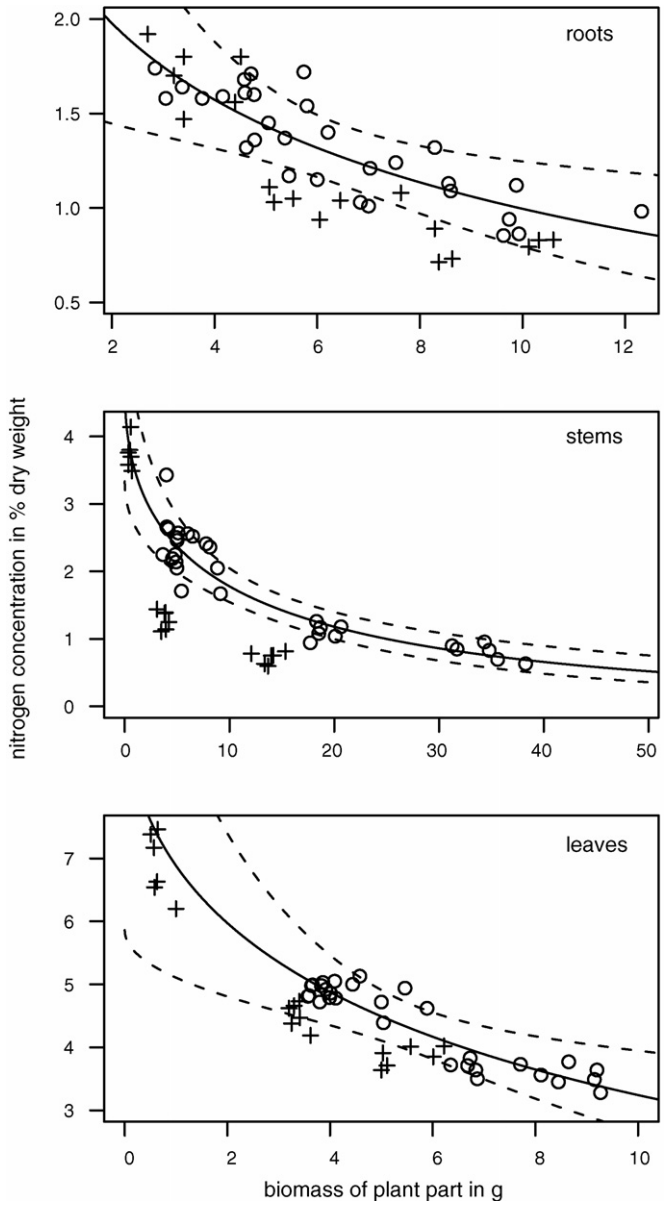

Fig. 4. The variation in plant nitrogen content between plant parts and with size. Control plants are shown as circles, treatment plants as +. The solid lines are models fitted to control data, and the dotted lines are 95% C.I.s around the fitted models.

similar pattern (data not presented). There was no evidence for soil nutrient levels limiting growth towards the end of the experiment. Growth rates suggest that control plants were still growing rapidly, and no symptoms of nutrient deficiency were recorded. The abundance of plant nitrogen continued to increase over the course of the experiment in both control and treatment plants. However, the total amount of nitrogen present in the control plants at the end of the experiment was much more than in the treatment plants and the removed shoot material put together (0.68 g versus 0.50 g, $t_{10} = 5.6$, $p < 0.01$). Therefore, if nutrients were limiting, they should tend to have had a larger impact on the control than the treatment plants.

Treatment plants after three weeks were of a similar total biomass to baseline plants ($t_{53} = 0.71$, $p > 0.1$), but they had a higher root and lower stem and leaf biomass (Table 2). Despite being of similar size, treatment plants after 20 days had much higher concentrations of WSC than baseline plants, particularly in the roots (Table 2). In fact, root WSC in treatment plants was similar to control plants of the same age. The non-WSC concentration in treatment plant roots was similar to the concentration in control plants, while the concentration in stems and leaves was more similar to that in baseline plants.

Date of sampling and plant size were highly correlated (Fig. 1). Therefore, the relationship between biomass and nutrients, for example, could be explained by different dates of sampling. When date of harvest was included as a fixed effect in a mixed effect model, there was no significant effect of plant size on nutrient status or plant phenology. However, as the range of biomasses on a given sampling day was small, these tests have an extremely low power. Independent of this, we have shown that alligator weed plants do not tend to a particular root to shoot

Table 2
The carbohydrate content of different plant parts

	Biomass (g)	Water soluble carbohydrate (% dry weight)	Non-water soluble carbohydrate (% dry weight)
Roots			
Baseline	4.78 ± 1.25 (a)	26 (22–31) (a)	3 (6–9) (a)
Treatment	5.55 ± 1.12 (b)	50 (46–53) (b)	13 (9–19) (b)
Control	6.98 ± 1.05 (c)	52 (50–54) (b)	18 (13–24) (b)
Stems and leaves			
Baseline	8.50 ± 1.23 (a)	15 (9–23) (a)	2 (1–6) (a)
Treatment	7.27 ± 1.08 (b)	25 (17–34) (b)	3 (1–6) (a)
Control	24.9 ± 2.50 (c)	48 (43–53) (c)	8 (5–12) (b)

Control and treatment plants were sampled after 20 days ($n = 8$ in each case). Biomass data are from baseline plants ($n = 40$), control plants ($n = 20$), and treatment plants ($n = 20$) harvested after 21 days (1S.D.s are shown). The mean and range of carbohydrate concentrations are shown. For each variable for each plant part, different letters indicate significant differences between baseline, control, and treatment plants (independent t-test, $p < 0.05$).

ratio for a given size, and shoot removal has a small effect on growth rate.

4. Discussion

By repeated destructive sampling, we were able to determine how a herbaceous plant regrows after mowing. While this method is labour intensive, it has highlighted several important aspects not detectable in other studies. If plant growth models are to be used to describe the phenology of resprouting, then they should take account of the nutritional effects of shoot removal (Table 1), as these can persist through time (Table 2 and Fig. 4). By fitting a growth curve to the control plants we could also predict plant growth based on different starting biomasses. Therefore, we could show that although treatment plants were smaller than the control plants after five weeks, treatment plants were of a similar biomass to that expected (i.e. to the biomass predicted for a plant of the same starting biomass as that of the below-ground parts of a control plant, Fig. 1). Shoot removal stopped biomass accumulation for about a week or so, but subsequent regrowth returned the treatment plants to the adjusted growth curve by the fourth week. Similar studies have shown that plants respond to pruning by preferentially allocating resources to return the plant to a particular ratio of plant parts (Poorter and Nagel, 2000; Zeng, 2003). However, alligator weed did not tend to the expected proportion of stem, leaf, and root within the time of this study (Figs. 2 and 3).

These results may still be consistent with the model of functional equilibrium—treatment plants were relatively nutrient poor and would be expected to have higher root biomasses (Agren and Franklin, 2003; Poorter and Nagel, 2000). The higher ratio of root to stem in treatment plants may be maintained until nutrients are assimilated to compensate for the high proportional loss of nutrients during disturbance and the nutrient dilution of plant tissue due to the speedy regrowth. The pattern of regrowth may also have adaptive value.

By regrowing with a higher root to shoot ratio and more stem than leaf biomass, subsequent shoot removals would be much less costly. Moreover, leaves produced after shoot removal were closer to the soil surface, making them less prone to similar damage. It is perhaps unsurprising that, despite alligator weed's palatability, cattle grazing has little effect on plants (Julien et al., 1992). The ability of alligator weed to resprout and change shape would have made the plant more resistant to grazing by South American herbivores (e.g. swamp deer, capybara, and rhea in its low elevation swampy habitats; and large extinct herbivores where they were prevalent).

While it is debatable whether the observed change in shape is evidence of an adaptive response to herbivory or simply an effect of reduced nutrition, the change in morphology does pose a problem for mechanical weed control. Even without considering the diminishing returns of multiple cuts, the data suggest that while mowing reduces biomass, it could only suppress plants if it was repeated more often than once a month (Fig. 1), a management option incompatible with the sensitive riparian and aquatic habitats that alligator weed invades (Julien et al., 1992). Unless competing vegetation shows over-compensation or mowing can be selective, at best mowing would be expected to maintain the competitive balance between alligator weed and other plants. The ease and speed with which small lengths of root were grown, albeit under very favourable conditions, also highlights the importance of plant fragmentation in the management of this weed.

The genus *Alternanthera* contains several species similar to *A. philoxeroides*, some of which have been spread around the world. Indeed part of the reason for the spread of *A. philoxeroides*, at least in Australia, is that it was used as a substitute for *A. sessilis*, a species used in Sri Lankan cuisine (Gunasekera and Bonila, 2001). Yet *A. philoxeroides* is the only one to have become a major invader. There appears to be little phylogenetic conservatism in species' ability to resprout (Vesk and Westoby, 2004b), and so it would be interesting to see whether resprouting ability is related to invasiveness in this genus. There are many potential traits for invasive species (for a review see Sakai et al., 2001). In the case of alligator weed, its remarkable ability to rapidly resprout may be one of the most important, and this ability can explain why alligator weed so readily invades grazed systems.

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